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The Disposition of *Trichopteris* (Cyatheaceae)

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The delimitation of genera and families has been a persistent problem in fern taxonomy, and the Cyatheaceae *sensu stricto* is no exception. Christensen (1905–06) adopted clearly artificial genera (*Cyathea, Hemitelia,* and *Alsophila*) based on complete (totally surrounding the sorus), partial, and absent indusia. He included *Lophosoria* and *Metaxya* in *Alsophila.* The latter two satellite genera are only distantly related to the major genera of the family, and nowadays are often placed in one or two families of their own.

Holttum (1963) proposed a single genus *Cyathea* for the Flora Malesiana region with two very distinct subgenera, *Sphaeropteris* and *Cyathea.* Holttum has maintained (1981, p. 466) that the "only subdivision of the genus clearly definable is that between subgenus *Sphaeropteris* and the rest." This indicates that *Alsophila* and *Cnemidaria* are less distinct from *Cyathea* than all three are from *Sphaeropteris,* which is confirmed by the lack of hybrids with *Sphaeropteris.* In studying the species of the Flora Malesiana region, Holttum came to the fundamental conclusion, among many, that indusium type is not an important generic character, for within a few species it varies widely.

Tryon (1970) divided the Cyatheaceae *sensu stricto* on the basis of scale characters, indusium presence or absence, and venation. He adopted the genera *Sphaeropteris* (scales conform), *Alsophila* and *Nephelea* (scales non-conform and setate), *Trichopteris* (scales non-conform and non-setate, laminae free-veined, and sori exindusiate), *Cyathea* (scales non-conform and non-setate, laminae free-veined, and sori indusiate), and *Cnemidaria* (scales non-conform and non-setate and laminae net-veined. According to Holttum and Edwards (1983, p. 179), this classification has assorted closely related species into *Cyathea, Sphaeropteris,* and *Trichopteris.* It is apparent that genera based on these characters are not natural.

Working from Tryon's (1970) generic concepts, I have found it possible to define readily recognizable and coherent genera in the Cyatheaceae *sensu stricto* by including in *Cyathea* the genus *Trichopteris* and the New World species considered to be *Sphaeropteris,* except for the *S. horrida* group. I accept the genera *Sphaeropteris, Alsophila* (including *Nephelea*), *Cyathea* (including *Trichopteris*), and *Cnemidaria.*

Occasional hybrids occur within *Alsophila* and *Cyathea* and between *Cnemidaria* and *Cyathea.* This is evidence of a greater degree of relationship than with *Sphaeropteris,* but in my opinion should not alone be the basis for adopting an inclusive *Cyathea* (either excluding or even including *Sphaeropteris*), for the characteristics of *Alsophila* and *Cnemidaria* are sufficiently different from those of *Cyathea* to distinguish the genera readily, and intergeneric hybrids in ferns are by no means rare and sometimes occur between large and supposedly separate genera (e.g., *Dryopteris* × *Polystichum*).

Sphaeropteris is almost entirely an Old World genus. Only *S. horrida* (Liebm.) Tryon and five allied species occur in the New World tropics. I agree with Holttum and Edwards (1983, pp. 161–162) in this delimitation. The other New World species that were placed in *Sphaeropteris* belong to *Cyathea*. In its restricted sense, this group was monographed by Tryon (1971). The stipe base scales of *Sphaeropteris* are distinct from those of all other New World Cyatheaceae genera in having cells of the same thickness and color from the central portion of the scales to the margin, except for some spreading, spinelike, often darker setae along the margins. The spores of *Sphaeropteris* bear flattened projections that are unique among New World Cyatheaceae (Gastony & Tryon, 1976). The laminae of *Sphaeropteris* are mostly 2-pinnate-pinnatifid (as in most *Cyathea* species), the pinnule segments are often falcate, and the abaxial surface is often pale and bears whitish scales on the abaxial surface. The scales of *Cyathea poeppigii* (Hook.) Domin [syn. *Sphaeropteris elongata* (Hook.) Tryon] and *C. myosuroides* (Liebm.) Tryon mimic those of *Sphaeropteris*, but are subtly different in their marginal body cells and setae (see key couplet 1).

Alsophila has over 200 species in the Old World and 30 (plus several hybrids) in the New World tropics. The New World species were monographed by Conant (1983), who correctly, in my opinion, included in the genus those species that had previously been monographed under the generic name *Nephelea* by Gastony (1973). The cells of the main body of the stipe base scales in *Alsophila* are not at all uniform, and at least an apical, spinelike seta, usually dark in color, is present; many species also have such setae along the lateral margins of the scales. The laminae are 2-pinnate-pinnatifid or more dissected and are often dark green; in some species the axes of the laminae are purplish-black.

Cyathea is the largest genus in the family. Many species occur in the Old World, and I count about 116 species in the New World. As I delimit the genus, it includes many species that have been placed in *Sphaeropteris* and *Trichopteris* by Tryon (1970). The species of *Cyathea* are treated by Tryon (1976), Windisch (1977, 1978), and Barrington (1978) under the aforementioned names. Most of the New World species have 2-pinnate-pinnatifid laminae; others (including a few diminutive species or depauperate specimens) are less divided, even merely pinnate-pinnatifid or pinnate. The sinuses between the segments or lobes are narrow and U-shaped, unlike those of many *Cnemidaria* species. The stipe base scales are concolorous or weakly to rather strongly bicolorous and lack marginal spinelike setae, and so differ from those of *Alsophila* and *Sphaeropteris*. They may have straight marginal cells and scales with entire margins, contorted marginal cells and scales with erose margins, elongate marginal cells and scales with fringelike margins, or, in a few cases, scales bearing marginal spinelike processes (see key couplet 1). The structure of these scales is a valuable character in assessing the relationship of species within the genus. The indusia vary from membranaceous and complete (sphaeropteroid) to firm and saucer-shaped (cyatheoid) to scalelike (hemitelioid) to absent.

Cnemidaria is an exclusively New World tropical genus that includes 25 species. It was monographed by Stolze (1974). The species of *Cnemidaria* have low, erect caudices and lack the tall, treelike trunks typically found in the other genera.

The veins are regularly anastomosing or nearly so, as stated in the key. The laminae are only pinnate-pinnatifid, with relatively low lobes or segments that have large, open, V-shaped sinuses between them. The abaxial surface of the laminae and its axes tend to be glabrous or nearly so with little variety in indument, unlike the foregoing genera. The spores are distinctive in being smooth (Stolze, pers. comm.) and in having three equatorial pores.

The species that have been placed in *Trichopteris* belong to several evolutionary lines and appear to be related to different species or species groups in *Cyathea*.

Cyathea atrovirens (Langsd. & Fisch.) Domin and *C. dichromatolepis* (Fée) Domin appear to have given rise to the series *C. miersii* (Hook.) Domin, *C. elegantula* Domin, and *C. corcovadensis* (Raddi) Domin, the type of the generic name *Trichopteris*. All have similar stipe base scales with contorted marginal cells and bullate and plane scales on the abaxial costae or costules. However, *C. corcovadensis* has the least lobed pinnae or pinnules and the fewest hairs on the adaxial surface of the costae and costules, a common correlation in "*Trichopteris*."

Cyathea sipapoensis (Tryon) Lellinger and *C. marginalis* (Klotzsch) Domin appear to be related to *C. macrocarpa* (Presl) Domin. All have similar stipe base scales that are concolorous, whitish, and with little cellular differentiation.

Two groups of "*Trichopteris*" species share rather strongly bicolorous rhizome scales with an elaborated, fringe-like margin. Almost all of these have conform apices, although not all have the apices articulate, another common correlation in "*Trichopteris*." I have not found likely ancestral species elsewhere in *Cyathea* for these groups, which may indicate their relative remoteness within the genus. In the pinnate group, *C. speciosa* Willd. appears to be least specialized and more like other species of *Cyathea* in having non-conform lamina apices; the related species are *C. cyclodium* (Tryon) Lellinger, *C. stolzei* A. R. Smith ex Lellinger, and *C. williamsii* (Maxon) Domin. All are subarborescent. In the bipinnate group, *C. petiolata* (Hook.) Tryon may be least specialized because it has non-conform apices and is clearly arborescent (caudices to 5 m); *C. conformis* (Tryon) Stolze and *C. intramarginalis* (Windisch) Lellinger also are arborescent, but have conform lamina apices. The remaining species are all subarborescent, with caudices usually less than 1 m long. *Cyathea intramarginalis* is related to *C. dissimilis* (Morton) Stolze; both share the character of l-forked veins, a reduction from the usual pinnate branching of the vein groups that terminates in *C. akawaiorum* Edwards, which has mostly simple veins. The other species of this group are *C. impar* Tryon and *C. steyermarkii* Tryon.

Key to the Genera of Neotropical Cyatheaceae *sensu stricto*

1. Cells of the stipe scales entirely uniform (the marginal and apical spinelike processes excepted), the cells along the margin not different from the central ones; spinelike processes present at the apex and margins of the stipe scales, these regular, antrorse, usually distant, and often dark; basal basiscopic vein of each vein group always arising from the costa; spores

bearing flattened, scalelike projections; indusia sphaeropteroid ..... *Sphaeropteris*

1. Cells of the stipe scales not entirely uniform, the cells along the margins slightly to markedly different in size, shape, wall thickness, or orientation from the central ones; spinelike processes absent (except in *Alsophila*, with strongly bicolorous scales and in *Cyathea poeppigii, myosuroides,* and *senilis,* with thinner-walled scales along the margins and irregular, often spreading, usually approximate spinelike processes), but approximate, thin, long, filamentous processes present in some species of *Cyathea*; basal basiscopic vein of each vein group not arising from the costa; spores bearing hairlike projections, granular deposits, or ridges, or nearly smooth; indusia cyatheoid, hemitelioid, sphaeropteroid, or absent.
2. Stipe scales provided with a dark (rarely pale) apical seta and sometimes lateral setae, the scales strongly bicolorous, the central band often several cells thick at the base; peripore of spores ridged ... *Alsophila*
2. Stipe scales lacking apical or lateral spinelike processes (approximate or rarely distant, lateral, rather thin setalike processes at entirely right angles to the axis of the scale present in a few species of *Cyathea,* especially in the *C. swartziana* group), the scales concolorous to weakly bicolorous, the central band usually only 1 cell thick at the base, the apex filamentous to round; perispore of spores not ridged.
3. Basal veins of each vein group forming regular areolae along the costae or the basal veins connivent to the base of the sinus or occasionally meeting the sinus just above the base; plants not arborescent; spores nearly smooth, bearing a single pore at or near the equator on each of the 3 sides; laminae mostly pinnate-pinnatifid with shallowly lobed pinnae and the sinuses between the lobes broadly V-shaped ..... *Cnemidaria*
3. Basal veins usually free and not connivent or anastomosing (except a transverse costal vein joining adjacent pinnate vein groups in *C. petiolata* and *williamsii*); plants arborescent or sometimes subarborescent; spores lacking equatorial pores; laminae mostly 2-pinnate-pinnatifid with deeply lobed pinnules and the sinuses between the lobes narrowly U-shaped ..... *Cyathea*

All of the species of the New World that had been placed in *Sphaeropteris* and most that had been placed in *Trichopteris* have valid names in *Cyathea.* For the few that do not, I wish to make the following combinations:

9910 **Cyathea axillaris** (Fée) Lellinger, comb. nov.—*Phegopteris axillaris* Fée, Gen. 9909 Fil. 243. 1852, effectively a nom. nov. based on *Polypodium axillare* Raddi, 21084 1819, non Aiton, 21083 1789.

9913 **Cyathea barringtonii** A. R. Smith ex Lellinger, nom. nov.—*Alsophila cordata* 9911 Klotzsch, Linnaea 20:441. 1847, non *Cyathea cordata* (Desv.) Mett. ex Diels 9912 in Engl. & Prantl, 1899.

9915 **Cyathea cyclodium** (Tryon) Lellinger, comb. nov.—*Trichopteris cyclodium* Tryon, 9914 Rhodora 74:446. 1972.

Cyathea demissa (Morton) A. R. Smith ex Lellinger, comb. nov.—*Alsophila demissa* Morton, Fieldiana, Bot. 28(1):7. 1955.

Cyathea dombeyi (Desv.) Lellinger, comb. nov.—*Alsophila dombeyi* Desv. Mém. Soc. Linn. Paris 6:320. 1827.

Cyathea gardneri (Hook.) Lellinger, comb. nov.—*Alsophila gardneri* Hook. Sp. Fil. 1:40. 1844.

Cyathea nanna (Barrington) Lellinger, comb. nov.—*Trichopteris nanna* Barrington, Rhodora 78:3, t. 1, f. 3, 4. 1976.

Cyathea pauciflora (Kuhn) Lellinger, comb. nov.—*Alsophila pauciflora* Kuhn, Linnaea 36:156. 1869.

Cyathea rufa (Fée) Lellinger, comb. nov.—*Alsophila rufa* Fée, Crypt. Vasc. Brés. 1:165. 1869.

Cyathea tryonorum (Riba) Lellinger, comb. nov.—*Alsophila tryonorum* Riba, Rhodora 69:66. 1967.

Cyathea venezuelensis A. R. Smith ex Lellinger, nom. nov.—*Trichopteris steyermarkii* Tryon, Rhodora 74:446, f. 11, 12. 1972, non *Cyathea steyermarkii* Tryon, 1972.

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